



# Oxygen, Ecology, and the Cambrian Radiation of Animals

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# **Oxygen, ecology, and the Cambrian radiation of animals**

Erik A. Sperling<sup>a,1</sup>, Christina A. Frieder<sup>b</sup>, Akkur V. Raman<sup>c</sup>, Peter R. Girguis<sup>d</sup>, Lisa A. Levin<sup>b</sup>,  
Andrew H. Knoll<sup>a,d,2</sup>

## **Affiliations:**

<sup>a</sup> Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA, 02138

<sup>b</sup> Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, 92093-0218

<sup>c</sup> Marine Biological Laboratory, Department of Zoology, Andhra University, Waltair, Visakhapatnam – 530003

<sup>d</sup> Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, 02138

<sup>1</sup> Correspondence to: [sperling@fas.harvard.edu](mailto:sperling@fas.harvard.edu)

<sup>2</sup> Correspondence to: [aknoll@oeb.harvard.edu](mailto:aknoll@oeb.harvard.edu)

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**The Proterozoic-Cambrian transition records the appearance of essentially all animal body plans (phyla), yet to date no single hypothesis adequately explains both the timing of the event and the evident increase in diversity and disparity. Ecological triggers focused on escalatory predator-prey ‘arms races’ can explain the evolutionary pattern but not its timing, whereas environmental triggers, particularly ocean/atmosphere oxygenation, do the reverse. Using modern oxygen minimum zones as an analogue for Proterozoic oceans, we explore the effect of low oxygen levels on the feeding ecology of polychaetes, the dominant macrofaunal animals in deep-sea sediments. Here we show that low oxygen is clearly linked to low proportions of carnivores in a community and low diversity of carnivorous taxa, while higher oxygen levels support more complex food webs. The recognition of a physiological control on carnivory therefore links environmental triggers and ecological drivers, providing an integrated explanation for both the pattern and timing of Cambrian animal radiation.**

/body

Cambrian fossils chronicle the appearance of essentially all high-level animal body plans, as measured by cumulative first appearances of metazoan phyla and classes, in a geologically-brief interval between ~540-500 million years ago (1, 2). Hypotheses to explain this event have commonly focused on either external controls, such as increasing oxygenation of the atmosphere-ocean system (1, 3-5), or internal controls based on an evolutionary, ecological or genomic breakthrough (2, 6-11). Recently, hypotheses in the latter category have emphasized the importance of macro-predation in facilitating observed increases in diversity and disparity across the Proterozoic-Cambrian transition (6-10).

External and internal controls have distinct attractions as triggers for Cambrian radiation. External controls relating to environmental oxygenation can explain the *timing* of the radiation— in other words, why animals radiated so dramatically beginning ~540 Ma, and not earlier or later. Indeed, the appearance of large, complex animals in the fossil record seems to follow directly on the heels of an Ediacaran increase and stabilization of marine oxygen levels as inferred from a number of different proxy records (reviewed by 12, 13). Such an environmental shift could remove a barrier to animal evolution, but aside from direct links to maximum permissible body size (14), it lacks an explicit mechanism to generate diversity (new species) and disparity (new body plans). There is no theoretical reason why ocean redox change should generate the evolutionary novelties—specifically the fundamentally new bauplans—seen in the Cambrian fossil record (15).

In contrast, ecological hypotheses focused on predation contain a clear driving mechanism for morphological innovation, namely selection pressures in evolving food

webs. They can also explain the origin and maintenance of high-level body plan disparity through the principle of frustration: organisms optimally suited to one task will be less well-suited for another, leading to a roughening of the fitness landscape and isolation of distinct fitness peaks (16). Consistent with this hypothesis, the origin of carnivory itself appears to be temporally correlated with the Proterozoic-Cambrian transition (Fig. 1), a prerequisite if predator-prey ‘arms races’ are to be viewed as the driving forces behind morphological innovation. In this discussion, we distinguish carnivory as mobile animal-animal interactions, as opposed to predation, which more broadly refers to one organism consuming another and may be as ancient as Eukarya (17). The oldest paleontological evidence for carnivory comes from circular perforations interpreted as drill-holes in the lightly-biomineralized metazoan fossil *Cloudina* from upper Ediacaran rocks in China (18). Strong evidence for carnivory can further be found in chaetognath fossils—voracious predators in the modern ocean—including the widespread early Cambrian skeletal fossil *Protohertzina*, interpreted as chaetognath grasping spines (19), and early Cambrian body fossils (20). Fossil aggregates and preserved gut contents in Cambrian Lagerstätten (for instance, hyolith shells in priapulid guts) provide additional fossil evidence for carnivory in early Cambrian oceans (21).

Support for the origin of carnivory near the Proterozoic-Cambrian boundary also comes from the qualitative mapping of feeding strategies onto a time-calibrated metazoan phylogeny (2). This suggests that the last common ancestor of bilaterians and the last common ancestors of the bilaterian super-clades Deuterostomia, Ecdysozoa and Lophotrochozoa were unlikely to have been carnivorous. Evolution of the carnivorous habit cannot be constrained with confidence on the tree until the origin of crown group

Nemertea (Fig. 1). Priapulids are another clade that likely evolved carnivory around the Proterozoic-Cambrian transition, although the timing can only currently be constrained between their divergence from kinorhynchs and the appearance of early Cambrian predatory forms (21), as the Priapulida crown group is undated and it is unclear whether the small, non-predatory forms at the base of this clade in morphological cladistics trees (22) represent the primitive form or are derived from a larger, potentially carnivorous ancestor. Molecular clock ages for nodes constraining the evolution of carnivory (2, 23) clearly suggest that bilaterians originated long before carnivory evolved within the clade around the Proterozoic-Cambrian transition (Fig. 1). Note that the derived nature of carnivory and the logic of phylogenetic systematics requires such a conclusion at some level regardless of the accuracy of molecular clock ages. A carnivory-based ecological hypothesis, then, can explain the *pattern* of morphological diversification seen in the Cambrian fossil record, but does not directly address its timing.

Based on a global study of feeding strategies in modern oxygen minimum zones (OMZs), we argue here that environmental and ecological hypotheses for Cambrian animal diversification are not decoupled, but can be linked through the lens of physiological constraint. Modern OMZs impinge on over  $10^6$  km<sup>2</sup> of seafloor (as determined at the  $< 0.5$  ml/l or  $22 \mu\text{M O}_2$  level) (24), and can serve as an analogue for ancient low-oxygen oceans (4, 25). In modern OMZs, the low-oxygen conditions are important in structuring the diversity and abundance of benthic communities (26-29). Some studies have considered how changing oxygen levels affect feeding strategies in individual basins, especially among polychaetes, but unlike studies of diversity (27), a global synthesis analysis of oxygen effects on carnivory has not been conducted.

## **Oxygen and carnivory in modern OMZs**

We assembled a data set comprising polychaete occurrences in low-oxygen ( $< 2$  ml/l  $O_2$ ;  $< 89 \mu M$ ) settings from below 150 m water depth. Water depth was constrained to be essentially beneath storm wave-base, thus removing the effects of atmospheric mixing, which cause fluctuating oxygen levels not necessarily represented during sampling. Only studies using a sieve size  $\leq 500 \mu m$  were used (30). Polychaetes were chosen as the study taxon for five reasons. First, they are the dominant macrofaunal taxon in deep-sea sediments and are especially abundant at low bottom-water oxygen concentrations, constituting up to 90% of the total fauna by abundance (26). Second, they exhibit a diversity of feeding strategies, including surface- and subsurface-deposit feeding, detritivory, filter feeding, carnivory, and even chemosymbiosis. Third, their feeding biology is relatively well understood (31), and although the feeding of most deep-sea polychaetes has not been observed *in vivo*, it is possible to code feeding strategies with reference to shallow-water relatives. Fourth, polychaetes are more tolerant of low oxygen levels than most other bilaterians, including arthropods and vertebrates (32, 26) and so constitute a conservative choice for our study. And finally, the use of a single group ensures that all taxa will have broadly similar physiologies and body plans, and observed trends will not be the result of ecological replacement by a different taxon with a fundamentally different bauplan. We note that similar correlations between oxygen and feeding ecology were found for the entire fauna in a single-basin investigation of the western Indian OMZ (33), suggesting that the results extend beyond polychaetes and are

unlikely to be specific to this clade.

A total of ten published studies were identified that met the oxygen, depth and sieve size requirements outlined above, resulting in a full data set that includes 962 polychaete species occurrences from 68 stations worldwide (Table 1). All species occurrences were coded for their likely feeding mode based on the literature, incorporating both classical observations and gut content analyses as well as new insights from tracer studies, stable isotopes, and fatty-acid analysis (see Supporting Information for full coding details). In some cases there was uncertainty in coding due to either contradictory information in the literature or low taxonomic resolution in faunal lists for higher taxa that are known to feed heterogeneously. In these cases, as well as for omnivorous taxa, we followed the logic of ref. (34) in counting these taxa as  $\frac{1}{2}$  carnivore for the purposes of calculating the number of carnivorous individuals in a fauna and the number of carnivorous taxa. Sensitivity analyses were then conducted wherein all uncertain and omnivorous taxa were coded as either entirely carnivorous or non-carnivorous (Table S2).

The percentage of carnivorous individuals in an assemblage and number of carnivorous taxa in an assemblage were binned for four different oxygen levels: Suboxia (0 - 0.2 ml/l O<sub>2</sub>, or 0 – 9  $\mu$ M; 26 stations), Severe Hypoxia (0.2 - 0.5 ml/l O<sub>2</sub>, or 9 – 22  $\mu$ M; 13 stations), Moderate Hypoxia (0.5 – 1.0 ml/l O<sub>2</sub>, or 22 – 45  $\mu$ M; 9 stations), and Mild Hypoxia (1.0 – 2.0 ml/l O<sub>2</sub>, or 45 – 89  $\mu$ M; 20 stations). Binning of stations was guided by Table 1 of ref. (35), which describes various O<sub>2</sub> thresholds currently used in the low-O<sub>2</sub> literature. We note that there are several different definitions for these thresholds, and, in particular, any definition of ‘Suboxia’ based on dissolved O<sub>2</sub>



concentration will encompass a variety of biogeochemical environments including many dominated by purely aerobic metabolisms (36; see Supporting Information for binning details). In addition to the ten studies analyzed quantitatively for the relationship between oxygen and carnivory, an unpublished data set from the Bay of Bengal, which contains additional very low-oxygen sites, was analyzed qualitatively for the presence-absence of carnivores.

Presence-absence data for carnivores across the data set illustrate a clear relationship to oxygen. Some carnivores can survive at low oxygen levels—but carnivores are only absent from an assemblage when oxygen falls below 0.34 ml/l (~15  $\mu$ M) (Fig. 2A). A similar pattern was seen in the Bay of Bengal (Table S1). The other investigated metrics for carnivory also show a relationship with oxygen levels (Fig. 2B and 2C). To test for significant differences in percent of carnivorous individuals and number of carnivorous taxa among oxygen levels, the data were log-transformed and compared using analysis of variance. Post hoc Tukey-Kramer tests ( $\alpha = 0.05$ ) were used to further explore significant differences among oxygen levels. Percent carnivorous individuals (Fig. 2B) increased dramatically between suboxic and hypoxic environments ( $F_{3,64} = 14.25$ ;  $P < 0.0001$ ). Indeed, half the suboxic stations had no carnivores at all. The striking relationship between oxygen and feeding ecology is further shown by comparing the number of carnivorous taxa present, a measure of food-web complexity, against oxygen (Fig. 2C). The number of carnivorous polychaete taxa in suboxic conditions was significantly lower than at higher oxygen settings ( $F_{3,64} = 20.4$ ;  $P < 0.0001$ ). These results are robust with respect to assumptions regarding feeding-mode uncertainty (Table S2). Although these analyses focus on oxygen, we recognize that

other environmental parameters and physiological stressors may be important in shaping the biology of modern oxygen minimum zones (26). Many potentially important variables, such as lower pH or high ammonium and sulfide levels in the sediment, can be ameliorated physiologically, although this typically requires an energetic expenditure (37). As aerobic respiration is the means by which animals regenerate the majority of their ATP, the ability to cope with these stressors thus largely remains linked to oxygen availability.

The global analysis of feeding strategies demonstrates a strong relationship between oxygen and the presence-absence of carnivores, the percentage of carnivores in an assemblage, and food-web complexity as measured by species diversity of carnivores. The precise reasons why carnivores are excluded from low-oxygen environments are not fully understood, but several (non-exclusive) possibilities can be considered. The ability to be a successful carnivore will relate fundamentally to the energy expended while catching and digesting prey versus the total energy gained. In general, macrofaunal abundances remain steady with respect to oxygen until they reach very low levels, below which organismal densities drop precipitously (26). The lack of predators at the very lowest oxygen stations may therefore simply be a function of extremely low prey densities. This possibility is countered by the lack of polychaete carnivores feeding on abundant meiofaunal nematodes that characterize OMZ cores (26). A physiological cause is likely required.

As there is a direct relationship between oxygen and maximum permissible body size (14), a second possibility is the higher oxygen requirement of larger body size. Given that most predators are larger than their prey, decreasing size with lower oxygen

levels (26, 38) may place a physiological limit on the ability of a carnivore to be larger than its prey. We suggest that the most likely reason for the dearth of carnivores in modern low-oxygen benthic environments is an inability to pay off the accumulated oxygen debt of a carnivorous lifestyle. Active carnivory, specifically capturing and subduing prey, is energetically costly (equals high oxygen demand) compared to either deposit or suspension feeding. In deposit and suspension feeding the mechanical costs of feeding are low and constant relative to total metabolism (39, 40). The metabolic cost of digestion (41) may also be important for low-oxygen settings. Filter and deposit feeders can maintain a continuous food input and thereby a more or less constant reduced carbon load in their gut. In contrast, many carnivores (especially those that engulf prey whole) are episodically faced with very large reduced carbon loads. Indeed, this observation forms the foundation of feeding mode inference from gut content analysis (e.g. ref. 31): deposit feeders and detritivores almost continuously have guts filled with sedimentary particles and detritus, whereas intermittently-feeding carnivores are usually characterized by empty guts. Together, active and muscular predation followed by digestion of a relatively large food item results in episodically high oxygen demand. The pelagic realm of modern OMZs is characterized by a diversity of carnivores that, in the cores of OMZs, usually migrate to more oxygenated water to pay off this oxygen debt (42). Interestingly, however, some permanently pelagic OMZ residents such as the vampire squid have adapted to low oxygen levels by losing the carnivorous feeding habit that is primitive for cephalopods and becoming detritivores (43). The inability to pay off an oxygen debt in the chronically low-oxygen benthos, where organisms are unable to migrate to higher-O<sub>2</sub> waters, represents the most likely explanation for the observation that polychaete

carnivore species diversity and percentage of the total fauna correlate with oxygen level.

## **Conclusions**

The observation that oxygen and feeding ecology are linked by physiology in the modern ocean suggests that ecological and environmental triggers for the Cambrian radiation can be integrated in a new causal hypothesis for Cambrian animal diversification. Modern OMZs indicate that low Proterozoic oxygen levels could have supported diploblastic animals and small, thin bilaterians (25), but also that any such animals in Neoproterozoic oceans would have been constrained to small sizes and to lifestyles and feeding modes that incur little oxygen debt. This would have limited both their fossilization potential and their capacity to drive evolutionary ‘arms races’ via carnivory. Rising oxygen levels would have allowed larger body sizes, but more importantly from a macroevolutionary standpoint, the first active, muscular carnivores. The establishment of stable redox conditions (44) (even if  $pO_2$  remained relatively low) may have been as important as the absolute magnitude of change itself, as unpredictable redox conditions would be deleterious to carnivores with the fluctuating oxygen demands described above. Escalatory arms races driven by these newly-evolved carnivores could then explain the relatively rapid expansion of metazoan diversity and disparity near the beginning of the Cambrian Period.

An Ediacaran transition in the availability of oxygen, allowing widespread carnivory, can thus explain both the timing and recorded biological pattern of Cambrian animal diversification. Specifically, the key physiological threshold in regards to the Cambrian radiation was likely not one of body size alone but rather ecological feeding

strategy. Given evolving physiologies through time, the specific oxygen levels at which ecological effects are seen in the modern may not directly relate to Proterozoic oceans. But since carnivory in polychaetes is limited at low oxygen levels despite being among the most low oxygen-tolerant taxa in the modern ocean (26, 32), with high-affinity respiratory pigments and good acid-base regulation—and 500 million years of natural selection doubtfully made carnivores less fit—it seems inescapable that low Proterozoic oxygen levels would have limited early animal food webs. Other factors besides carnivory and oxygen may have been important, but many of them are related to carnivore evolution itself (for instance the evolution of sensory apparatus and vision — ref. 11). This focus does not obviate a role for developmental genetics, but as most gene families that govern bilaterian development originated well before Cambrian body-plan diversification (2, 45), the prime role of development was in assembling these pre-existing genes into coherent networks to build body plans suited to the evolving Cambrian fitness landscape. The primary question in this integrated causal hypothesis now remains the timing and absolute magnitude of hypothesized late Neoproterozoic oxygenation. Continued exploration of the causes, timing and magnitude of oxygenation will provide further insight into the role of oceanographic change in the evolution of carnivory and this unique geobiological event. Further study of the relationship between feeding ecology and oxygen in modern OMZs, as well as the co-evolutionary history of animals and ocean redox state in deep time, may also help us predict future changes associated with ocean deoxygenation and expanding oxygen minimum zones (46).

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## Figure Legends

**Fig. 1.** The temporal origins of carnivory in animals. A) Geological time scale for the Cryogenian-Ordovician (Ord.). B) and C) Origins of carnivorous metazoans as inferred from the molecular (refs. 2 and 23) and fossil records. In panel B), red horizontal whiskers represent maximum estimates for the evolution of carnivory in nemerteans and priapulids as constrained by molecular clock ages for their divergence from non-carnivorous sister groups. Red circles represent minimum ages for carnivory as constrained by the nemertean crown group (1), as all extant nemerteans are carnivores, and early Cambrian priapulid fossils (2) with gut contents indicating a carnivorous habit. Carnivory evolved between these minimum and maximum age estimates. In panel C), fossil evidence for carnivory around Precambrian-Cambrian transition includes apparent drill holes in the fossil *Cloudina* (3); the trace fossil *Treptichnus pedum*, if it represents

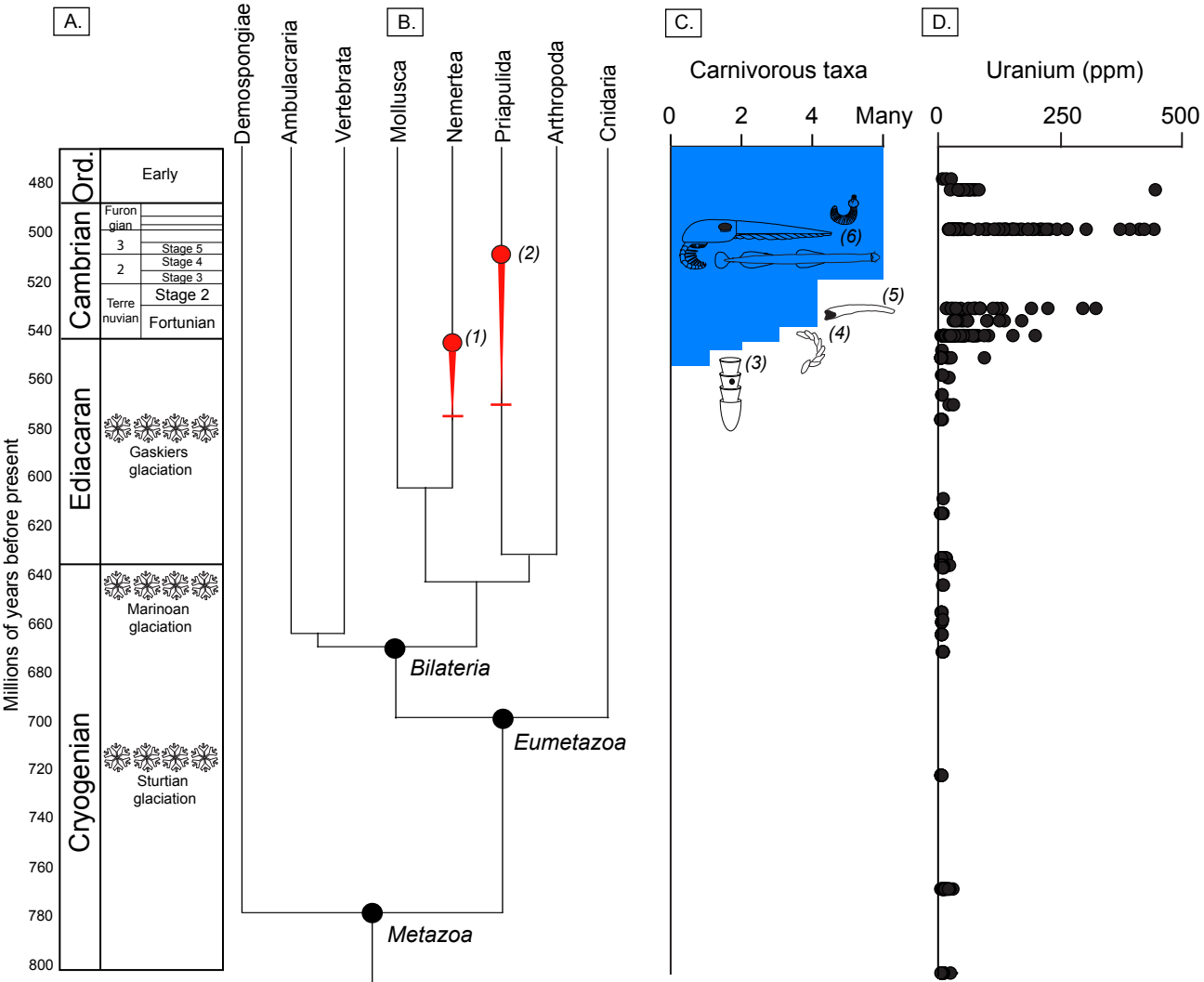
the burrowing activities of carnivorous priapulids (ref. 47 and see note in main text) (4); and the widespread early Cambrian small shelly fossil *Protohertzina*, interpreted as grasping spines of chaetognaths (ref. 19) (5). By Series 2 and 3 of the Cambrian, fossil Lagerstätten record numerous carnivores including a variety of arthropods, priapulids with hyolith gut contents, and chaetognath body fossils (6); reviewed by ref. (21). D) The origin of carnivory coincides with a major increase in the concentration of uranium and other redox-sensitive trace elements in organic-rich, fine-grained sedimentary rocks (data replotted from ref. 48). Higher values indicate higher seawater concentrations of U and more widespread oxygenation. Other redox proxies for this interval are reviewed by refs. 12 and 13.

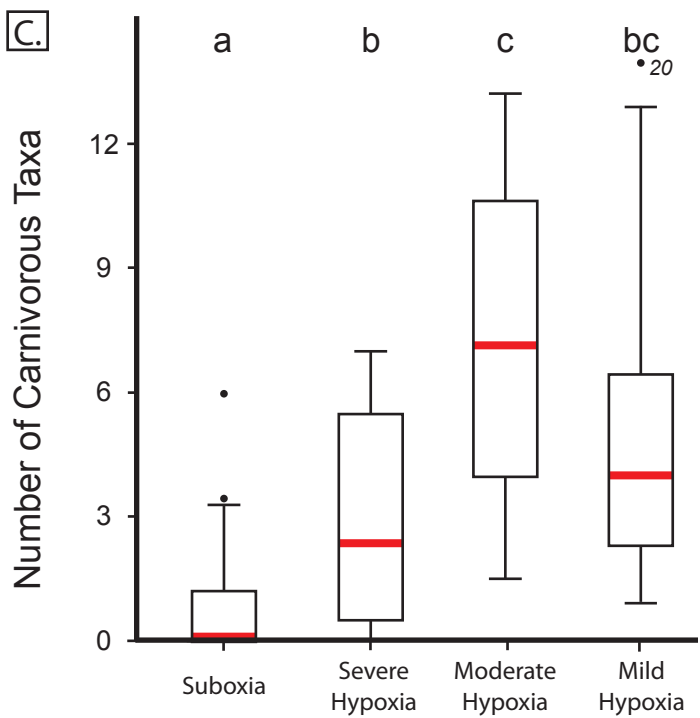
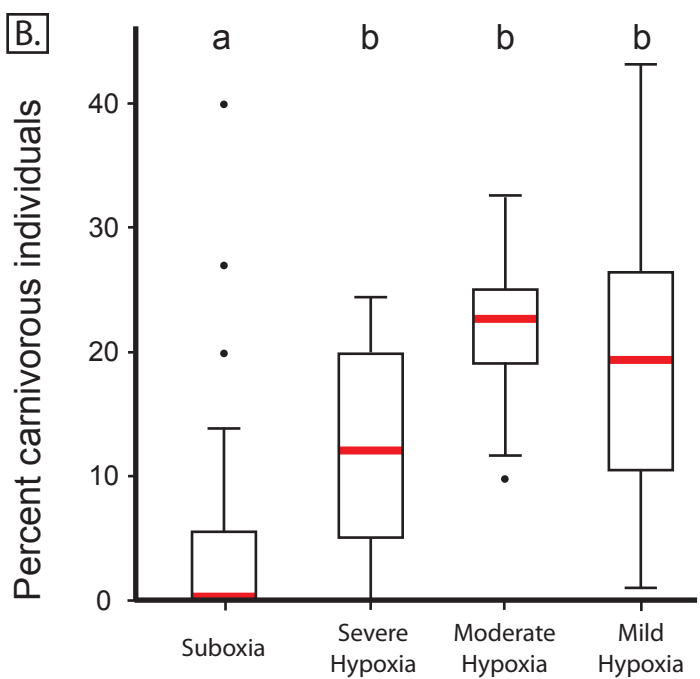
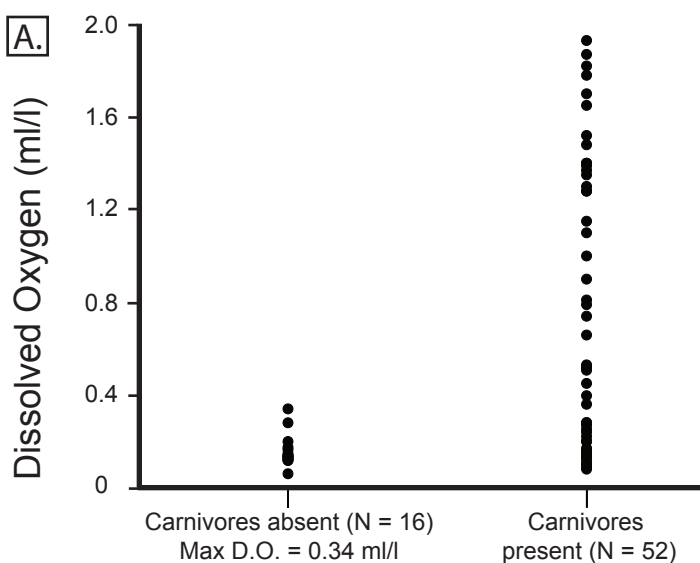
**Fig. 2.** Relationship between oxygen and carnivory in modern oxygen minimum zones.

A) Bottom-water oxygen concentrations at stations with carnivores present and absent.

D.O. = Dissolved Oxygen. B) and C) Standard box-and-whisker plots of percent carnivorous individuals (B) and number of carnivorous taxa (C) against four oxygen bins: Suboxia (0 - 0.2 ml/l O<sub>2</sub>, or 0 – 9 µM; 26 stations), Severe Hypoxia (0.2 - 0.5 ml/l O<sub>2</sub>, or 9 – 22 µM; 13 stations), Moderate Hypoxia (0.5 – 1.0 ml/l O<sub>2</sub>, or 22 – 45 µM; 9 stations), Mild Hypoxia (1.0 – 2.0 ml/l O<sub>2</sub>, or 45 – 89 µM; 20 stations). For box plots, the box encompasses the 1<sup>st</sup> and 3<sup>rd</sup> quartiles, thick bar depicts the median, and whiskers depict true minimum and maximum values except where outliers (dots) greater than 1.5 times the interquartile range were identified. Means with the same lower-case letter at the top of the graph are not significantly different based on Tukey's HSD test ( $P = 0.05$ ). Outlier in Mild Hypoxia bin in (C) not to scale.

Fig. 1





**Table 1.** Studies analyzed herein. Number of stations refers to the stations within the specified depth and O<sub>2</sub> range investigated here and not the total number of stations in a given study. Oxygen concentrations reported as in the published studies (ml/l O<sub>2</sub>); for reference 0.2 ml/l ~ 9 umol/kg ~ 0.29 mg/l ~ 9 matm (see also ref. 35).

Study	Reference Number	Margin	Number of stations	Oxygen range (ml/l)
Diaz-Castefiada and Harris, 2004	49	Baja California, Mexico	6	1.0 - 1.4
Vetter and Dayton, 1998	50	Southern California	5	0.45 - 1.39
Levin et al., 2010; unpublished	51	California and Oregon	9	0.22 - 0.66
Levin et al., 2000	52	Oman	5	0.13 - 0.52
Hughes et al., 2009	53	Pakistan	8	0.1 - 1.78
Gallardo et al., 2004	54	Central Chile	2	0.13 - 0.52
Palma et al., 2005	55	Chile	11	0.06 - 1.93
Levin et al., 2009	56	Pakistan	16	0.117 - 0.2
Levin et al., 1991	57	Volcano 7, off Mexico	3	0.09 - 0.81
Ingole et al., 2010	27	Western Indian	3	0.08 - 1.35
A. Raman, unpublished	-	Bay of Bengal	38	0.01 - 1.19

## **Supporting Information**

### **Oxygen, ecology, and the Cambrian radiation of animals**

Erik A. Sperling<sup>a,1</sup>, Christina A. Frieder<sup>b</sup>, Akkur V. Raman<sup>c</sup>, Peter R. Girguis<sup>d</sup>, Lisa A. Levin<sup>b</sup>, Andrew H. Knoll<sup>a,d</sup>

#### **Affiliations:**

<sup>a</sup> Department of Earth and Planetary Sciences, Harvard University, Cambridge, MA, 02138

<sup>b</sup> Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, 92093

<sup>c</sup> Marine Biological Laboratory, Department of Zoology, Andhra University, Waltair, Visakhapatnam – 530003

<sup>d</sup> Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, 02138

<sup>1</sup> Correspondence to: [sperling@fas.harvard.edu](mailto:sperling@fas.harvard.edu)

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## Supporting Information Materials and Methods

### *Station binning*

The total number of stations investigated in this study was 106. Binning of stations was guided by Table 1 of Hofmann et al. (2011; ref. 35), which describes various  $O_2$  thresholds currently used in the low- $O_2$  literature. As the goal of this study was to investigate how an increase in oxygen might affect feeding ecology in a low-oxygen world, the upper limit for the study was set at 2.0 ml/l  $O_2$ , classified by ref. 32 as the onset of hypoxia for normal marine fauna. Note that there are several definitions for the onset of hypoxia in the literature (reviewed by ref. 35). We used the most inclusive definition, but the first bin here also encompasses other definitions for the onset of hypoxia, including the ‘classic’ definition of hypoxia of 2.0 mg/l  $O_2$  (~ 1.42 ml/l  $O_2$ ) and the median lethal concentration in a comprehensive literature review (1.6 ml/l  $O_2$ ) (58). The first bin (mild hypoxia) ranged from the onset of hypoxia at 2.0 ml/l  $O_2$  to moderate hypoxia (1.0 ml/l  $O_2$ ), or the point at which many invertebrates exhibit sublethal responses such as arm tipping in ophiuroids or extension from the sediment in sea anemones (59). The second bin (moderate hypoxia) ranged from moderate hypoxia to severe hypoxia (0.5 ml/l  $O_2$ ), where mass mortality occurs in shallow marine faunas (32). The third bin (severe hypoxia) ranged from the onset of severe hypoxia to the onset of suboxia (0.2 ml/l  $O_2$ ) (60), or the point at which non-oxygenic heterotrophy (‘suboxic’ metabolisms) begins to dominate. The fourth bin (suboxia) ranges from the onset of suboxia to absolute anoxia at 0 ml/l  $O_2$ . As with the onset of hypoxia, there are several possible definitions in use for this ‘suboxic’ or biogeochemical boundary. This boundary was delineated as 0.2 ml/l  $O_2$  by Tyson and Pearson (1991; ref. 60). In recent years, it has generally shifted towards 0.1 ml/l  $O_2$  or 5  $\mu$ M (see Table 1 of Hofmann et al., 2011; ref. 35). However, in either case, these values are arbitrary—see extended discussion by Canfield and Thamdrup (2009; ref. 36). Specifically, anaerobic processes such as nitrate reduction are often essentially absent (as measured by the lack of a nitrite peak) well below 0.1 ml/l or 5  $\mu$ M  $O_2$ , while in other cases these processes occur at far higher oxygen levels; there is no direct relationship between oxygen levels and the onset or dominance of anaerobic microbial respiration. We have chosen the onset of our ‘Suboxia’ bin at the original 0.2 ml/l  $O_2$  level (60), and acknowledge that this will represent a variety of biogeochemical environments, including many dominated by purely aerobic metabolisms (36). Binning the low-oxygen data into two separate bins based on the alternate 5  $\mu$ M  $O_2$  boundary (e.g. 0 – 0.114 ml/l  $O_2$  and 0.114 – 0.2 ml/l  $O_2$  bins) did not produce significant differences in the means for either percent carnivorous taxa in a fauna (student’s two-tailed t-test,  $P = 0.14$ ) or number of carnivorous taxa present ( $P = 0.78$ ). As the combined ‘Suboxia’ bin is significantly different from the higher-oxygen bins (Fig. 2, Table S2), choice of bins based on alternate definitions for suboxia does not appear to be affecting the results.

Despite sampling all known studies with available faunal lists that met our criteria, most of the very low oxygen (< 0.2 ml/l  $O_2$ ) stations were located in the Indian Ocean, specifically the Pakistan margin, the Oman margin, and the Bay of Bengal (see Supporting Data set 1). As current sampling for the lowest-oxygen bin is restricted geographically, the possibility remains that some of the effects seen at the very lowest oxygen levels are

related in part to geography. One very low oxygen site on the Chilean margin (295 meter station of ref. 55; 0.06 ml/l O<sub>2</sub>) has no carnivores, suggesting that the relationship between carnivory and oxygen is not a purely geographical effect. Further testing the influence of geography will require more detailed oceanographic sampling of very-low oxygen regions outside the Indian Ocean.

### *Feeding mode coding*

As discussed in the main text, polychaetes were chosen to examine the relationship between oxygen levels and metazoan feeding ecology for several reasons. In addition to these reasons, polychaetes have been shown to be a good exemplar group for the entire fauna (61).

Regarding taxon inclusion or exclusion in faunal lists examined, taxa identified only as Polychaeta were excluded as their feeding modes are not codable. Oligochaetes and siboglinids, which are phylogenetically “polychaetes” (62) were included. Other phyla such as echiurans and sipunculans that are often associated with annelids in molecular phylogenies and may in fact be included within Polychaeta (62), but which have fundamentally different bauplans, were not included. In reality, the inclusion or exclusion of these four higher taxa will not affect the results, as they are all relatively rare in these data sets and all non-carnivorous.

Coding polychaete feeding strategies is facilitated by the compilation of Fauchald and Jumars (1979; ref. 31), which has been highly cited and utilized both by polychaete workers and in general ecology studies. The key insight of this compilation is that feeding ecology in polychaetes is generally conservative at the family level. Thus, given even a rough taxonomic assignment, an organism’s likely feeding strategy can be determined. Although this compilation is over three decades old, the general pattern has, notwithstanding some new insights, stood the test of new observations and new methods, including light stable isotopes (63-67), fatty-acid analysis (68), labeled tracer studies (69), gut architecture studies (70), and new gut content analyses (71) (but see ref. 72 for syllids which suggests the possibility of a more omnivorous lifestyle for the Eusyllinae).

Many studies simply adopt the coding in Table XXXI of Fauchald and Jumars (ref. 31; likely with high accuracy considering how well the classification scheme has held up to further research). However, some carnivorous groups (see below) can be heterogeneous in their feeding strategies, and thus the finer taxonomic resolution in published faunal lists can better help guide coding. Here, for each species occurrence, a google search was conducted at the lowest taxonomic resolution possible (genus or species) using the searches “*Genus species*” + feeding, and “*Genus species*” + diet. In cases where no information could be found for a specific species, or the faunal list identified the organism to the generic level only, data for other species within that genus were used. In these cases, preference was generally given to geographically-closer congeners. In some cases, conflicting information was found for a given genus, leading to uncertainty in coding (see below).

Although we attempted to extend beyond Fauchald and Jumars (ref. 31) and incorporate local and more recently-published data at a lower taxonomic level into our coding, it should be noted that there may be some circularity. Specifically, many studies discuss or code the feeding strategies of polychaetes with reference to Fauchald and Jumars (1979; ref. 31). Nonetheless, scientists working in a specific geographical locale can be expected to have a strong understanding of the natural history of the fauna, and



although Fauchald and Jumars (1979; ref. 31) will remain a starting point, new insights into the local fauna will be incorporated through time into more recent publications. As knowledge of the feeding strategies of polychaetes grows (especially for deep-sea polychaetes), it is likely that the codings for some of these taxa will change. But as with any large synthesis, errors are expected to be randomly distributed (e.g. ref. 73), and it is unlikely that the overall pattern will change with additional observations (see also sensitivity analyses with respect to coding uncertainty in *Table S2*).

In addition to references listed above (refs. 31, 63-72) and information in the studies themselves (refs. 27, 49-57), references 74-142 were additionally used in guiding coding (see Supporting Data set 1).

Complete environmental data and faunal lists for each station, with references justifying each coding decision, and annotations regarding the references and any uncertainty in coding, are contained in Supporting Data set 1. Faunal lists and their codings for each study are contained in individual tabs within the excel file. The raw count data are presented in the same format as provided by the Authors of each study to retain their original structure.

#### *Uncertainty in coding feeding modes*

Several sources of uncertainty exist in coding feeding modes. First, many organisms are simply omnivorous, or opportunistic, and do not fit easily into defined feeding categories (143, 144). Some polychaete families show a tendency towards omnivory, for instance the Onuphidae (25). These taxa are coded as omnivores, and as described in the main text, we followed the logic of Jumars and Fauchald (1977; ref. 34). Each taxon was counted as  $\frac{1}{2}$  carnivore for the purposes of calculating the number of carnivorous individuals in a fauna and the number of carnivorous taxa. For other taxa, contradictory information was found in the literature. This was most common when the taxonomic resolution in faunal lists extended only to the generic level, and our coding was based on other species in the genus. It is possible that heterogeneity of feeding modes exists within the genus, but also possible that many of these species exhibit a degree of omnivory. When faced with contradictory information from the literature, these taxa were coded as Carnivore(?). Taxa coded as Carnivore(?) were also counted as  $\frac{1}{2}$  carnivore in Figure 2 of the main text. Thus, taxa coded as either Omnivore or Carnivore(?) are functionally the same in the statistical analysis, but represent true evidence for omnivory in the former and uncertainty in coding in the latter. As an example, amphinomids are generally considered carnivores (31), but there is stable isotope evidence (e.g. ref. 63; *Paramphinome*) and tracer studies (e.g. ref. 145; *Linopherus*), sometimes combined with lipid evidence (146) indicating that some deep-sea amphinomids are deposit feeders or detritivores. Therefore species identified in faunal lists simply as Amphinomidae sp. were coded as Carnivore(?). On the other hand, studies of gut contents in the amphinomid *Chloeia pinnata* from the Southern California borderland (98) demonstrated that this species feeds on both animals and detritus, and the diet varies based on the time of year. As there is species-level information available for this taxon, this species in the Del Mar margin and La Jolla Canyon data sets of Vetter and Dayton (1998; ref. 50) was coded as an omnivore. Species that are primarily scavengers were not coded as carnivores, although it is recognized that some may feed opportunistically as carnivores.

A second source of uncertainty, as hinted above, is low taxonomic resolution in

faunal lists. Most polychaete families are conservative in their feeding strategies and can be coded according to Table XXXI of Fauchald and Jumars (1979; ref. 31). This is particularly true for many of the filter feeding families (such as the Serpulidae and the Sabellariidae) and the deposit feeding families (for instance the Ampharetidae, Capitellidae and Cossuridae as three examples). Others exhibit heterogeneity in feeding mode but remain non-carnivorous (for instance the Spionidae some of which can switch between surface-deposit feeding and suspension feeding (87, 88)). Many of the carnivorous families are entirely carnivorous, although in some, like the hesionids, the meiofaunal members and members at vents and seeps are not and feed on bacteria or diatoms (31). In a few groups, though, specifically the Amphinomidae, Dorvilleidae, Eunicidae, Lumbrineridae, Nereidae, Phyllodocidae and Syllidae, there is strong evidence for non-carnivorous feeding habits in some but not all species (ref. 31; and see references listed above). Consequently, taxa identified, for instance, only as “Nereidae sp.” or “Unidentified Syllidae” in faunal lists cannot be coded with confidence. Such taxa were also coded as Carnivore(?).

As a final point, this coding strategy results in conservative coding for polychaetes at the very lowest oxygen levels. Specifically, there is evidence that many of the typically ‘carnivorous’ polychaete groups switch to omnivorous or non-carnivorous habits at very low oxygen levels. For instance, the amphinomid *Linopherus* on the Pakistan OMZ can feed as a carnivore or scavenger, but feeds in large part on phytodetritus at very low O<sub>2</sub> (145, 146). Isotopic studies have recently demonstrated that jawed dorvilleid polychaetes from Costa Rican methane seeps feed primarily on prokaryotes, specifically Archaea (136). It is likely that dorvilleids (and also the jawed hesionids) at very low oxygen levels are feeding on microbes, especially in settings where large, filamentous, sulfide-oxidizing mats occur. Thus, although such taxa are conservatively coded as Carnivore or Carnivore(?) if the taxonomy is not well-resolved, in reality this coding is potentially incorrect and they are non-carnivorous. In other words, given current knowledge Fig. 2 likely overestimates the number of carnivorous taxa and percent carnivorous individuals present in a fauna in the Suboxia bin. As there is no such bias affecting the higher-oxygen bins, the difference between low- and high-oxygen stations is probably even greater than our coding suggests. Future stable isotopic, fatty acid analysis, pulse-chase labeling experiments and gut content analyses of putative carnivores living at very low oxygen levels will be instrumental in providing more concrete constraints on the diets of these organisms.

## Supporting analyses

### *Bay of Bengal data set*

In addition to the ten published studies analyzed quantitatively for the statistical relationship between oxygen levels and carnivory (Fig. 2 and Table S2), we coded and investigated a macrofaunal data set from the Bay of Bengal. This data set has previously been discussed by ref. 29 and has led to important inferences about the relationship between environmental parameters and ecological responses in this region (29). However, this data set was investigated qualitatively here for carnivore presence-absence rather than being included in the quantitative synthesis for several reasons. First, the full data set and details of sampling remain unpublished (Raman et al., in preparation). Second, the study was conducted using a Smith-McIntyre grab instead of a coring device as in the other studies. For a number of reasons from possible loss of mud to unequal sampling with depth due to the bite of the grab (see review by ref. 147), the results are less quantitative

(or rather, it is more difficult to monitor the quality of each sample) than multi-cores. Finally, the size of the data set (orders of magnitude more than many of the other studies) is problematic from a statistical point of view; inclusion of this study would dwarf the others and lead to strong geographical biases.

The Bay of Bengal data set is valuable to consider in the context of oxygen and carnivory, though, because it includes many sites at the very lowest end of the oxygen spectrum (suboxia bin of Figure 2). Importantly, it includes five stations below 0.10 ml/l O<sub>2</sub>—an alternate threshold for suboxia (35)—as compared to only three stations below this level in the remainder of the data set. As the observation that carnivores are rare or absent in suboxia is based on a relatively small sampling of the seafloor compared to the total area bathed by low-O<sub>2</sub> waters, this data set provides an opportunity to examine other stations in this bin.

Station	Depth	Dissolved Oxygen	Polychaete density (individuals/m <sup>2</sup> )	Carnivorous individuals per m <sup>2</sup>	Percent carnivores	Carnivorous taxa
190 DP 203	203	0.01	270	0	0.00	0
604 BRU 150	150	0.01	70	10	14.29	1 ( <i>Ancistrosyllis parva</i> )
191 DP 152	152	0.03	710	0	0.00	0
198 KKD 150	150	0.03	70	0	0.00	0
206 BRU 201	201	0.03	50	10	20.00	1 ( <i>Aphroditid</i> sp. 1)
72 VSKP S1 207	207	0.12	9635	20	0.21	2 (Polynoinae UI and Pilgardi SI)
75 BRU S1 228	228	0.13	1390	10	0.72	1 (Pilgardi SI)
81 PDP S1 254	254	0.15	8955	10	0.11	1 (Pilgardi SI)
79 CLK S3 537	537	0.18	518	4	0.72	0.5 ( <i>Leptonereis</i> sp.)
69 KKD S1 202	202	0.19	511	6	1.08	2 (Polynoinae UI and <i>Hermonia hystrix</i> )

**Table S1:** Stations in the Suboxia bin (< 0.20 ml/l O<sub>2</sub>) from the Bay of Bengal data set.

Examination of these data demonstrate that stations in the Suboxia bin from the Bay of Bengal exhibit the same pattern seen in other very low-O<sub>2</sub> stations, with low percentages of carnivores relative to the entire fauna, and low (0-2) numbers of carnivorous taxa present. Stations 66 DP S1 202 (0.20 ml/l O<sub>2</sub>) and 78 CLK S2 202 (0.23 ml/l O<sub>2</sub>) also have no carnivores present. Therefore, the Bay of Bengal data set provides additional support for the hypothesis that low-O<sub>2</sub> sites are characterized by low percentage of carnivores and low species diversity of carnivorous taxa

### *Testing the effect of uncertainty in feeding mode coding*

To test whether omnivory, contradictory information in the literature, or low taxonomic resolution in faunal lists was affecting the results, two sets of sensitivity analyses were conducted. In the first, all taxa coded as Omnivore or Carnivore(?) were coded as Carnivore. In the second, all taxa coded as Omnivore or Carnivore(?) were coded as Non-Carnivore. As described in the main text, to test for significant differences

in percent of carnivorous individuals and number of carnivorous taxa among oxygen levels the data were log-transformed and compared using analysis of variance. Post hoc Tukey-Kramer tests ( $\alpha = 0.05$ ) were used to further explore significant differences among oxygen levels.

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#### A. Full data set

##### % Carnivores (log-transformed)

Source	DF	SS	MS	F-ratio	P	
Oxygen	3	9.18	3.06	14.25	<0.0001	post hoc Tukey HSD: a,b,b,b suboxia, severe, moderate, mild
Error	64	13.75	0.21			
Total	67	22.93				

##### Carnivorous Taxa (log-transformed)

Source	DF	SS	MS	F-ratio	P	
Oxygen	3	4.73	1.58	20.4	<0.0001	post hoc Tukey HSD: a,b,c,bc suboxia, severe, moderate, mild
Error	64	4.95	0.08			
Total	67	9.68				

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#### B. Sensitivity analyses

##### % Carnivores (log-transformed) - coding uncertainty as carnivorous

Source	DF	SS	MS	F-ratio	P	
Oxygen	3	9.78	3.26	13.36	<0.0001	post hoc Tukey HSD: a,b,b,b suboxia, severe, moderate, mild
Error	64	15.61	0.24			
Total	67	25.4				

##### Carnivorous Taxa (log-transformed) - coding uncertainty as carnivorous

Source	DF	SS	MS	F-ratio	P	
Oxygen	3	5.26	1.75	20.03	<0.0001	post hoc Tukey HSD: a,b,b,b suboxia, severe, moderate, mild
Error	64	5.61	0.09			
Total	67	10.87				

**% Carnivores (log-transformed) - coding uncertainty as non- carnivorous**

Source	DF	SS	MS	F-ratio	P	
Oxygen	3	9.4	3.13	13.32	<0.0001	post-hoc Tukey HSD: a,ab,c,bc suboxia, severe, moderate, mild
Error	64	15.05	0.24			
Total	67	24.44				

**Carnivorous Taxa (log-transformed) - coding uncertainty as non-carnivorous**

Source	DF	SS	MS	F-ratio	P	
Oxygen	3	4.22	1.41	18.02	<0.0001	post-hoc Tukey HSD: a,a,b,b suboxia, severe, moderate, mild
Error	64	4.99	0.08			
Total	67	9.21				

**Table S2: Results of ANOVA and post hoc Tukey HSD tests. A). Data in Fig. 2 of the main text (uncertain taxa coded as ½ carnivore following Jumars and Fauchald, 1977; ref. 145) B). Sensitivity analyses coding either all omnivorous or uncertain taxa as carnivores, of all omnivores and uncertain taxa as non-carnivores.**

The analyses demonstrate that the results are robust with respect to the strategy for coding uncertainty as implemented here. Specifically, under all coding schemes, the percent carnivorous individuals in a fauna and number carnivorous taxa for the Suboxia bin (or Suboxia + Severe Hypoxia) are significantly lower than the remaining higher-oxygen bins. The different coding strategies do have some effect on which specific bins are significantly different.

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Counts are individuals per m<sup>2</sup>

190 DP 203 191 DP 152

Taxa					190 DP 203	191 DP 152
	Family	Feeding Mode	Source	Notes	203	152
Acrocirrda (UI)	Acrocirridae	SDF	Fauchald and Ju	Some may be SS	0	0
Amagebioculata	Ampharetidae	SDF	Fauchald and Jumars, 1979		0	0
Amphaeritid (sp)	Ampharetidae	SDF	Fauchald and Jumars, 1979		0	70
Amphaeritid (sp)	Ampharetidae	SDF	Fauchald and Jumars, 1979		0	0
Amphinomid (s)	Amphinomidae	Carnivore?	Fauchald and	Many deep-sea	0	0
Amphinomid (s)	Amphinomidae	Carnivore?	Fauchald and	Many deep-sea	0	0
Chloeia rosea	Amphinomidae	Carnivore?	Fauchald and Ju	Chloeia rosea. Fi	0	0
Pseuderythoe	Amphinomidae	Omnivore	Fauchald and	According to the	0	0
Hermonia hystri	Aphroditidae	Carnivore	Fauchald and Ju	The possibility	0	0
Hermonia sp.	Aphroditidae	Carnivore	Fauchald and Ju	The possibility	0	0
Polynoinae (UI)	Polynoidae	Carnivore	Fauchald and Jumars, 1979		0	0
Aphroditid sp1 (	Aphroditidae	Carnivore	Fauchald and Ju	The possibility e	0	0
Aphroditid sp2 (	Aphroditidae	Carnivore	Fauchald and Ju	The possibility e	0	0
Aphroditid sp.3	Aphroditidae	Carnivore	Fauchald and Ju	The possibility e	0	0
Aphroditid sp.4	Aphroditidae	Carnivore	Fauchald and Ju	The possibility e	0	0
Capitellid (Ins)	Capitellidae	SSDF	Fauchald and Jumars, 1979		0	0
Notomastus sp.	Capitellidae	SSDF	Fauchald and Jumars, 1979		0	0
Capitellid (Sh)	Capitellidae	SSDF	Fauchald and Jumars, 1979		0	0
Mediomastus sp	Capitellidae	SSDF	Fauchald and Jumars, 1979		0	0
Cirratulid sp.1 (S	Cirratulidae	SDF	Fauchald and Jumars, 1979		0	0
Cirratulid sp.2 (S	Cirratulidae	SDF	Fauchald and Jumars, 1979		0	0
Cirratulid (Ins)	Cirratulidae	SDF	Fauchald and Jumars, 1979		0	0
Cirratulid sp.1 (S	Cirratulidae	SDF	Fauchald and Jumars, 1979		0	0
Cossura coasta	Cossuridae	SDF	Blake, 1993		200	600
Disoma orissae	Trochochaetidae	SDF	Fauchald and Ju	According to Wc	0	0
Diopatra neapol	Onuphidae	Omnivore	Fauchald and Ju	Fauchald and Ju	0	0
Eunice sp.1 (Ins)	Eunicidae	Carnivore	Fauchald and Ju	Genus Eunice is	0	0
Eunice sp.2 (Sh)	Eunicidae	Carnivore	Fauchald and Ju	Genus Eunice is	0	0
E. pinnata (sh)	Eunicidae	Carnivore	Fauchald and Ju	Presumably still	0	0
Eunice indica	Eunicidae	Omnivore	Cheung et al. (20	Genus Eunice is	0	0
Eunicid (SI)	Eunicidae	Carnivore?	Fauchald and Ju	Many eunicids n	0	0
Nematonereis sj	Eunicidae	Carnivore	Grall et al., 2006	Fauchald and Ju	0	0
Lumbrineres sp	Lumbrineridae	Carnivore?	Fauchald and	Lumbrinerids	0	0
Lumbrineres sp	Lumbrineridae	Carnivore?	Fauchald and	Lumbrinerids	0	0
Lumbrineres sp	Lumbrineridae	Carnivore?	Fauchald and	Lumbrinerids	0	0
Lumbrineres sp	Lumbrineridae	Carnivore?	Fauchald and	Lumbrinerids	0	0
Lumbrineres sp	Lumbrineridae	Carnivore?	Fauchald and	Lumbrinerids	0	0
Lumbrineres lat	Lumbrineridae	Carnivore?	Grall et al., 2006	Grall et al. (2006	0	0
L. notocirrata (S	Lumbrineridae	Detritivore	Sarkar et al., 2005		0	0

Marphysa sp.	Lumbrineridae	Carnivore?	Fauchald and Ju Different Marph	0	0
Ninoe chilensis	Lumbrineridae	SSDF	Sanders et al., 1962; Gaston, :	0	0
Onuphis dibranc	Onuphidae	Omnivore	Fauchald and Jumars, 1979	0	0
O. investigatoris	Onuphidae	Omnivore	Fauchald and Jumars, 1979	0	0
Protodorviella sj	Dorvilleidae	Carnivore?	Fauchald and Jumars, 1979	0	0
Flabelligerid (Ins)	Flabelligeridae	SDF	Fauchald and Jumars, 1979	0	0
Flabelligerid (Sh)	Flabelligeridae	SDF	Fauchald and Jumars, 1979	0	0
Stylarioides ben	Flabelligeridae	SDF	Fauchald and Ju Should be in a d	0	0
Glycera oligodor	Glyceridae	Carnivore	Fauchald and Ju F+J: the carnivor	0	0
Glycera sp1 (Sh)	Glyceridae	Carnivore	Fauchald and Ju F+J: the carnivor	0	0
Glycera sp2 (Sh)	Glyceridae	Carnivore	Fauchald and Ju F+J: the carnivor	0	0
Glycera sp.3 (Sl)	Glyceridae	Carnivore	Fauchald and Ju F+J: the carnivor	0	0
Pilargid (Sl)	Pilargiidae	Carnivore	Fauchald and Jumars, 1979	0	0
Anscistrostylis p	Pilargiidae	Carnivore	Fauchald and Jumars, 1979	0	0
Hesionid (UI)	Hesionidae	Carnivore	Fauchald and Ju Small hesionids	0	0
Heterospio sp. (	Heterospionidae	SDF	Fauchald and Ju Very little is kno	0	0
Magelona sp.	Magelonidae	SDF	Fauchald and Jumars, 1979	0	0
Maldanid (UI)	Maldanidae	SSDF	Fauchald and Jumars, 1979	0	0
Nephtys dibranc	Nephtyidae	Carnivore	Grippio et al., 20 Web searches st	0	0
N. gravieri	Nephtyidae	Carnivore	Fauchald and Jumars, 1979	0	0
Nephtys sp. (Sh)	Nephtyidae	Carnivore	Fauchald and Jumars, 1979	0	0
Nephtys sp. (slo)	Nephtyidae	Carnivore	Fauchald and Jumars, 1979	0	0
Leonnates sp. (	Nereidae	Omnivore/Filter	Riegl and Purkis, In "Coral Reefs c	0	0
Leptonereis sp.	Nereidae	Carnivore?	Fauchald and Ju No generic infor	0	0
Nereid (UI Sl)	Nereidae	Carnivore?	Fauchald and Ju Nereids are ofte	0	0
Nereis sp.1 (Ins)	Nereidae	Carnivore?	Fauchald and Ju Nereids are ofte	0	0
Nereis sp.2 (Sh)	Nereidae	Carnivore?	Fauchald and Ju Nereids are ofte	0	0
Ophelina sp	Opheliidae	SSDF	Fauchald and Jumars, 1979; Wur	0	0
Orbinid (Sl)	Orbiniidae	SSDF	Fauchald and Jumars, 1979	0	0
Orbinid (Ins)	Orbiniidae	SSDF	Fauchald and Jumars, 1979	0	0
Orbinid (Sh)	Orbiniidae	SSDF	Fauchald and Jumars, 1979	0	0
?Aricidea sp.	Paraonidae	SDF	Levin et al., 1 Aricidea may sel	0	0
Aricidea sp.	Paraonidae	SDF	Levin et al., 1 Aricidea may sel	0	0
Paraonis sp. (Ins)	Paraonidae	SDF	Fauchald and Jumars, 1979	0	0
Paraonis sp. (SL)	Paraonidae	SDF	Fauchald and Jumars, 1979	0	0
Paraonis sp. (sh)	Paraonidae	SDF	Fauchald and Jumars, 1979	0	0
Pectinarid sp.1 (	Pectinariidae	SSDF	Fauchald and Jumars, 1979	0	0
Pectinarid sp.2 (	Pectinariidae	SSDF	Fauchald and Jumars, 1979	0	0
Eteone sp. (sl)	Phyllodocidae	Carnivore?	Gaston (1987); † Different specie	0	0
Phyllodocid (UI,	Phyllodocidae	Carnivore?	Fauchald and J Levin et al. (19	0	0
Phyllodocide lor	Phyllodocidae	Carnivore	Fauchald and Jumars, 1979	0	0
Pisionid (UI)	Pisionidae	SSDF	Fauchald and Ju Not much inform	0	0
Sabellid sp.1 (In	Sabellidae	FF	Fauchald and Jumars, 1979	0	0
Sabellid sp.2 (Sh)	Sabellidae	FF	Fauchald and Jumars, 1979	0	0
Sabellid sp.3 (sl)	Sabellidae	FF	Fauchald and Jumars, 1979	0	0
Prionospio sp. (I	Spionidae	SDF/FF	Dauer, 1985 Dauer (1985) stu	0	0

Prionospio sp1	Spionidae	SDF/FF	Dauer, 1985	Dauer (1985) stu	70	30
Prionospio sp2	Spionidae	SDF/FF	Dauer, 1985	Dauer (1985) stu	0	0
Prionospio pinn	Spionidae	SDF/FF	Dauer, 1985	Dauer (1985) stu	0	0
P. cirrobranchia	Spionidae	SDF/FF	Dauer, 1985	Dauer (1985) stu	0	0
Laonice cirrata (	Spionidae	SDF	Cheung et al., (2008); Maurer an		0	0
Malacoceros ind	Spionidae	SDF	Dauer and Ewing, 1991		0	0
Polydora sp.1 (lr	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Polydora sp.2 (S	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Polydora sp.3 (S	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Pygospio sp. (sh	Spionidae	SDF/FF	Fauchald and Jumars, 1979		0	0
Scolecipis indica	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Spionid sp2 (Sh	Spionidae	SDF	Fauchald and Jumars, 1979		0	10
Spionid sp1 (Sh	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Spionid sp. (SL)	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Spionid sp3 (Sh	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Spionid sp4 (Sh	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Spionid sp5 (Sh	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Spionid sp6 (Sh	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Spiophanes sp.	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Spiohanes bomt	Spionidae	SDF	Fauchald and Jumars, 1979		0	0
Sternaspis scuta	Sternaspidae	SSDF	Cheung et al., 2008; Shelley et al		0	0
Syllid (UI)	Syllidae	Carnivore?	Maurer and \	Many syllids :	0	0
Pista sp. (Ins)	Terrebellidae	SDF	Fauchald and Jumars (1979);		0	0
Streblosoma pei	Terrebellidae	SDF	Fauchald and Jumars, 1979		0	0
Steblosoma sp. (	Terrebellidae	SDF	Fauchald and Jumars, 1979		0	0
Terebellid sp.1 (	Terrebellidae	SDF	Fauchald and Jumars, 1979		0	0
Terebellid sp.2 (	Terrebellidae	SDF	Fauchald and Jumars, 1979		0	0
Terebellid sp.3 (	Terrebellidae	SDF	Fauchald and Jumars, 1979		0	0
Terebelid sp.4 (S	Terrebellidae	SDF	Fauchald and Jumars, 1979		0	0
Poecilochaetus :	Poecilochaetida	SDF/FF	Fauchald and Jumars, 1979; Che		0	0
Poecilochaetus :	Poecilochaetida	SDF/FF	Fauchald and Jumars, 1979; Che		0	0
Polychaete (UI S	Not coded				0	0
Oligochaetes	Oligochaeta	Detritivore/Dep	Brusca and Brusca, 2003		0	0



[illegible]



30	210	30	0	0	0	0
0	0	0	40	0	20	70
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0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	10
0	0	0	0	0	0	0
0	0	0	0	0	0	0



[illegible]

0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	55	0	10	0	815	0
0	25	0	20	8	7207.5	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
10	0	0	0	0	0	0
0	0	10	0	10	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	290	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	2.5	0	0
0	0	0	7.5	0	2.5	0
0	0	0	0	0	0	0
0	0	0	0	0	5	47.5
0	0	0	0	0	0	0

75 BRU S1 22 81 PDP S1 25 83 PDP S1 95 66 DP S2 184 68 DP S2 950 69 KKD S2 19 71 KKD S2 85

75 BRU S1 228	81 PDP S1 254	83 PDP S1 953	66 DP S2 184	68 DP S2 950	69 KKD S2 197	71 KKD S2 850
228	254	953	184	950	197	850
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	2.5	0	0	2.5
0	0	0	0	0	0	0
0	0	2.5	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	5	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	12.5	0	0
175	152.5	2.5	27.5	0	112.5	5
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	2.5	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	10	0	0	0	12.5
0	0	0	0	0	0	0
0	0	0	0	0	0	0

[illegible]

0	0	0	0	0	0	0
0	0	0	0	0	0	0
35	292.5	2.5	2.5	0	7.5	0
1170	8500	2.5	2.5	3	10	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	15	2.5	12.5	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	2.5	0	62.5	0	0
0	0	0	0	0	0	0

72 VSKP S2 1074 VSKP S2 8175 BRU S2 1978 CLK S2 20179 CLK S2 61081 PDP S2 2183 PDP S2 95

72 VSKP S2 168	74 VSKP S2 858	75 BRU S2 192	78 CLK S2 202	79 CLK S2 610	81 PDP S2 215	83 PDP S2 953
168	858	192	202	610	215	953
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	5	0	0	0	0
0	0	0	0	0	0	0
0	0	2.5	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	7.5	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	1925	0	0
565	0	0	0	0	0	2.5
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	2.5	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0



[illegible]

	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	30	340	2.5	0
65	0	980	1475	30	595	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	10	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	2.5
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	3	0
0	0	0	0	0	0	0



[illegible]

0	0	0	0	0	0	0
0	0	0	0	0	0	0
55	0	0	150	25	117.5	95
135	17.5	1087.5	0	4480	0	2830
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	10	0	0	0	10	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0
2.5	0	0	0	0	0	0
0	0	0	0	0	0	0
0	5	0	0	0	0	0
0	0	0	0	0	0	0
0	0	0	0	0	0	0

82 PDP S3 538

82 PDP S3 538

538

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172.5

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## 12.5

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[illegible]

**O O 50 O O O O O O O O O O O O O O O O O O O**